

MORPHOLOGICAL INVESTIGATION IN TWO MODER-HUMUS PROFILES AND THE ROLE OF THE SOIL FAUNA IN THEIR GENESIS

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(Received July 23, 1969)

SUMMARY

The humus profile is defined as the morphologic feature in the soil profile as a result of the decomposition of litter beginning at its deposition on the soil surface and ending with mineralization.

Macro- and micromorphologically, two humus profiles arisen from litter from Red oak and from Douglas fir respectively were studied.

From the two humus profiles the soil-fauna was analysed. The feeding-biology of the most important saprophagous species was studied in cultures. Not only the choice of food was determined but especially morphologic characteristics as feeding-patterns and excrements were noted. With the aid of these results the genesis of both humus profiles could be explained. The influence of the quality of the litter upon the composition of the soil fauna, the speed of devouring the litter ("Vermoderung") and the way in which the soil fauna consumes the litter was obvious.

Two phenomena are especially studied. These are specifically "ageing" of excrements and displacement of organic particles in the humus profile.

INTRODUCTION

Numerous small animals are found in the soil. It is well-known that a number of them play an important part in the organic-matter cycle and, in all probability, also in the formation of stable, high-grade humic acids.

Litter under a layer of natural vegetation breaks down in accordance with a certain pattern, presenting a characteristic morphological type (profile), referred to as "humus form" or, less frequently, "humus type". In view of the prevailing confusion and the possibility of assigning different meanings to these terms - viz. (1) humus form as a profile (Kubiens, 1953, pp.26,27,37-50; 1955) as opposed to humus form as a horizon within that profile (Ramann, 1911, pp.171-177, 192-195); and (2) humus type as a profile (Hartmann, 1965, pp.8-9) opposed to humus type as a horizon within that profile (Jongorius and Schelling, 1960) - we prefer here to speak of the "*humus profile*", which we use to indicate the profile that develops as a

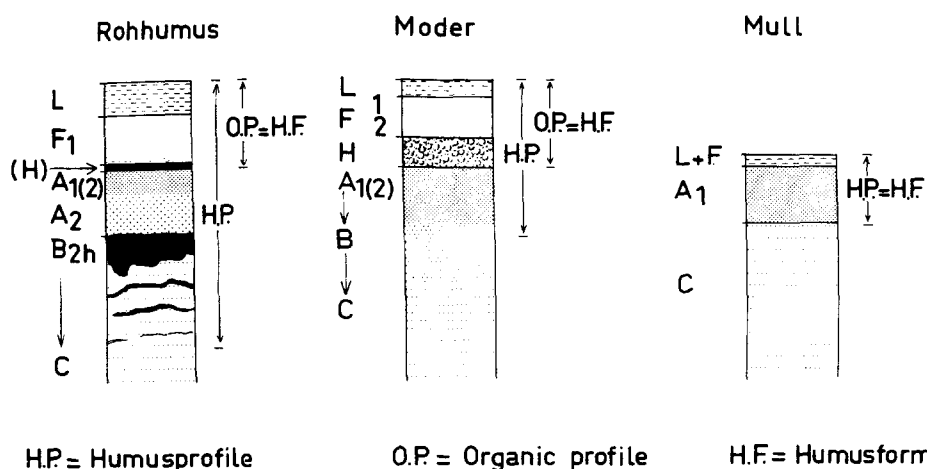


Fig.1. Humus profile: the profile that develops as a result of the breakdown of litter, whose upper limit has the shape of an L-layer ($L + F_1 = O_1$ or A_{00}) and whose lower limit has the shape of a horizon, in which the last remains of the organic matter are mineralized.

result of the breakdown of litter, whose upper limit has the shape of an L layer ($L + F_1 = O_1$ or A_{00}) and whose lower limit has the shape of a horizon, in which the last remains of the organic matter are mineralized. The humus profile lies partly *on* and partly *in* the mineral soil. The section lying on the mineral soil may be termed the *organic profile* (see Fig.1).

It will strike the reader that the definition of the humus profile describes the entire decomposition of litter while some humus forms, e.g., "Rohhumus" and "Moder" (Kubiena, 1953) only describe the decomposition of litter as far as this takes place on the surface of the mineral soil. Then the humus form is identical with the organic profile.

There is justification for postulating that the vertical sequence of humous layers in the humus profile is pedogenetic, with the living organisms in the soil, and the soil fauna in particular, engendering a soil-forming process: the consumption of litter and the formation of excrements. We, therefore, speak advisedly of (F and H) "horizons", which may for a large part consist of faecal material¹. The L layer is not a horizon, for the leaves falling from the trees eventually arrive in the L layer, after having been borne along by the wind. We might call this layer an aeolian sediment,

¹Coprogenous material and coprogenous horizon are terms frequently encountered (Ramann, 1911; Kubiena, 1953; Jongerius, 1961 and others). Kopros (Greek) means dung. Coprogenous means literally "caused by excrement", though what is actually meant is that the horizon is built up out of excrements; in other words it is zoogenous and the excrements are not coprogenous particles but "zoogenous particles". That is why the term coprogenous has been avoided here; we shall speak of "faecal material", "faecal pellets" or "excrements" instead.

which is then geogenetic. Since the material stored in the L layer (together with dead roots) is the source from which the humus profile develops, we can speak of "parent material".

The object of the investigation was to study the genesis of the humus profile and to find an answer to the questions: "What part does the soil fauna play in the genesis of the humus profile? What is the nature of this fauna and what factors influence it?" To this end research was carried out on a profile under Red oak and one under Douglas fir and the results compared.

The two profiles investigated are drifts of preglacial coarse sand to sand respectively (according to the "Soil Survey Manual", 1951) unaffected by groundwater and so susceptible to drought. The pH figures are practically the same for both humus profiles and vary from 3.30 to 3.80. Since the system in the organic profile is not known, it was thought preferable to measure the pH in water instead of in a normal solution. Moreover the samples were not dried beforehand.

The choice of the plots was determined by the desire, to keep the number of variables low. For instance, the distance between the two plots has been kept as short as possible (20 m). There were no weeds or underbrush (homogeneous litter).

The profiles lie in the "De Warnsborn" estate (owned by the "Het Gelders Landschap" Society), situated between Oosterbeek and Schaarsbergen in the municipality of Arnhem.

METHODS EMPLOYED IN THE RESEARCH

The research can be divided into four distinct stages:

(1) Macromorphological description of the profile; qualitative micro-morphological analysis with the aid of mammoth-sized thin sections made by using Vestopal-H (Jongerijs and Heintzberger, 1963); analysis of the soil texture and measurement of pH values.

(2) An orientational fauna analysis to gain some idea of the composition of the soil fauna. A Berlese-Tullgren funnel was used to determine the presence of Enchytraeidae was determined by immersing the soil sample in a funnel filled with water and by heating the water from above by a 100 W lamp. (Van der Drift, 1949; Kevan (editor), 1955, pp.313-412; Schaller, 1962; Murphy (editor), 1962).

Size of the sample (superficies):

Macro-Arthropoda and earth-worms	50 × 50 cm
Micro-Arthropoda	25 cm ²
Enchytraeidae	100 cm ²

(3) Culture and observation of the most important animal inhabitants. The object of culturing the fauna is to establish its activity in the breakdown of the litter. Special attention was given to morphological characteristics. For instance, feeding patterns, but excrements in particular, may be characteristic and so afford an opportunity of identifying the fauna active in breaking down the litter.

Excrements may be characterized by shape, size, consistency, colour and composition. For the latter it is important whether or not macrophytic

TABLE I

Analysis of the dry matter in the humus profile below Red oak (Fig. 3)¹

Depth (cm)	Horizon	Percentages of the different quantities ²																Percentages			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	organic- free soil	Percentages cavities >30μ
0.5-1	F1	12.5	12.5	2.5	0.0	2.0	0.0	1.0	0.5	0.0	0.0	0.0	0.0	3.0	3.5	0.5	0.5	1.0	0.0	2.5	58.0
1-2	F2	0.5	7.5	5.5	3.0	3.0	11.0	1.5	3.0	1.5	0.0	0.0	1.0	1.5	5.0	0.5	1.5	3.0	0.0	3.0	48.0
2-3	F2	0.0	3.0	2.0	4.0	0.5	1.5	4.5	3.5	1.3	2.0	0.0	1.5	0.5	10.0	2.0	2.0	5.0	0.0	1.2	55.5
3-4	H	0.0	0.5	0.0	0.5	0.5	0.0	3.0	2.0	1.5	3.0	2.0	11.5	0.0	7.5	3.0	3.0	5.5	0.0	0.0	56.5
4-5	H	0.0	0.0	0.0	0.5	0.0	0.0	4.0	4.0	1.0	2.0	1.5	5.0	0.0	6.5	2.5	3.0	3.5	0.0	0.0	66.5
5-6	H	0.0	0.0	0.0	0.8	0.0	0.0	3.5	2.0	0.0	1.5	1.0	7.5	0.0	7.5	1.5	1.0	4.5	0.0	6.5	62.7
6-7	A1(2)	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	1.0	1.0	6.5	45.0	44.0

¹ The amounts are expressed in percentages of the soil volume.

² Explanation of numerals 1 - 18: (1) microbiologically affected leaves; (2) leaf attacked by fauna; (3) intact excrements of small *Diptera* larvae, mainly Mycetophilidae; (4) ageing excrements of Mycetophilidae- and Tipulidae-larvae (sometimes as a result of severe fungal attack); (5) ageing faecal masses of Mycetophilidae- and Tipulidae-larvae (sometimes as a result of severe fungal attack); (6) ageing faecal masses of Mycetophilidae- and Tipulidae-larvae (sometimes as a result of severe fungal attack); (7) non-differentiated faecal masses without tissue remnants, quite possibly derived from *Dendrobaena rubida*; (8) ageing of the masses mentioned in (7) by penetrating fungi; (9) exposed *Oribatei* excrements (probably from *Nothrus silvestris*); (10) ageing, broken down *Oribatei* excrements; (11) intact excrements from *Dendrobaena rubida*; (12) ageing faecal masses of *Dendrobaena rubida*; (13) faecal mass of Enchytraeidae and *Onychiurus quadricellatus*; (14) root or branch attacked by fauna; (15) root or branch attacked by *Oribatei*; (16) roots not attacked, often living; (17) root periderm filled by fungi with black humic substances; (18) faecal parts illuviated in the mineral soil.

*Ageing is defined on p.28.

TABLE II

Analysis of the dry matter in the humus profile below Douglas fir (Fig. 10)¹

Depth (cm)	Horizon	Percentages of the different quantities ²																					Percentage organic- free soil	Percentage cavities >30μ	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21			
0-1	L	16.0	10.5	3.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.5	3.5	0.0	0.0	0.0	0.5	0.0	1.0	64.0
1-2	L	15.0	6.5	10.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	1.0	4.0	0.0	0.0	0.0	0.5	0.0	0.0	61.5
2-3	F1	15.5	4.5	16.5	4.0	0.0	1.0	0.0	4.0	0.0	0.5	0.0	0.5	0.0	0.0	2.5	2.5	0.0	0.0	0.0	0.5	0.0	0.0	0.0	48.0
3-3.5	F2	10.0	2.5	7.0	8.0	2.0	2.0	1.5	7.0	4.0	0.0	2.5	0.5	0.0	1.0	2.0	8.0	0.0	0.0	2.5	1.0	0.0	0.5	0.0	38.0
3.5-4.5	F2	4.0	1.0	3.0	5.0	5.0	4.0	4.0	5.5	5.0	0.0	1.0	0.5	1.0	4.5	0.5	4.0	1.5	3.0	0.0	2.0	0.0	1.0	0.0	44.5
4.5-5.0	H	0.0	0.0	0.5	0.5	2.0	6.5	7.0	0.0	5.0	0.0	0.0	1.0	8.0	8.0	0.0	5.0	0.0	0.0	5.0	5.5	0.0	0.0	0.0	46.0
5.0-5.5	H	0.5	0.0	0.5	0.2	5	3.0	3.0	1.5	4.5	0.0	0.0	1.5	12.5	8.5	0.0	3.5	0.5	0.0	0.0	3.5	0.0	8.5	0.0	46.0
5.5-6.5	A1(2)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	1.5	12.5	60.0	0.0	24.5

¹ The amounts are expressed in percentages of the soil volume.

² Explanation of numerals 1 - 21: (1) anatomically intact needles; (2) the parenchyma has almost entirely disappeared as a result of microbiological attack; (3) fragmented needles; (4) needles partly mined by Phthiracaridae; (5) needles entirely mined by Phthiracaridae and filled with excrements; (6) exposed Phthiracaridae excrements; (7) ageing Phthiracaridae excrements, adhering to each other*; (8) intact Mycetophilidae larvae excrements; (9) ageing Mycetophilidae larvae excrements; (10) intact Tipulidae larvae excrements; (11) ageing Tipulidae larvae excrements; (12) intact *Adelta* larvae excrements; (13) ageing *Adelta* larvae excrements; (14) mixture of ageing excrements; (15) faecal mass of Enchytraeidae; (16) roots attacked by fauna; (17) root or branch entirely mined by Phthiracaridae and filled with excrements; (18) root or branch attacked by Phthiracaridae; (19) roots not attacked, often living; (20) root periderm filled by fungi with black humic substances; (21) faecal parts illuviated in the mineral soil.

*Ageing is defined on p.28.

and microphytic material (*primary particles*)¹ and mineral particles are present. The position of the excrements in the profile, for instance their being scattered or their lying in nidi, is also important in this connection.

In addition to establishing the foregoing we also paid attention to the fauna's behaviour.

The saprophagans to be cultured were chosen on the basis of the fauna analysis; those assumed to play an active part in the breakdown of the litter were the ones eligible for selection. They were cultured on material from the various horizons of both profiles. They were cultured in Petri dishes, the upper edge of which was treated with "Fluon", a substance which, having dried, presents such a smooth surface that the creatures cannot possibly escape (Elton and Holleman, 1965). The dishes were placed in a dark room and kept at a constant temperature of 15°C, special attention being given to the prevention of desiccation. The fauna was observed for a period of three months, feeding patterns noted and excrements collected and studied. The latter both in glycerine preparations (determining the fragmentation of the litter) and in undisturbed condition in thin sections of approx. 4 cm².

(4) Quantitative determination of the various components in the thin section in accordance with the "point-counts method" (Jongorius, 1963). By this method a blank section of the same size as the thin section is placed under the thin section. The blank section is divided into quadrants of 0.5 × 0.5 cm. With the aid of an integration eyepiece (magnifying 8 times), in which 25 points are marked out in a grid to form equilateral triangles, 25 point-counts are now identified in the thin section within each quadrant and noted. If the total number of point-counts which have been measured is put at 100% it can be represented in a graph as a function of the depth. In this way 8.450 point-counts were identified per section, the results of which are shown in Tables I and II. (The interpretation is given later see sections on genesis of humus profiles under Red oak and Douglas fir, soil morphologically characteristic fauna, and spatial building up of moder humus profiles.

Studies such as those described under (2) and (3) were made to try to identify the tracks of the fauna in the profile (1) and subsequently to quantify them (4).

DESCRIPTION AND GENESIS OF THE HUMUS PROFILE UNDER RED OAK (*Quercus borealis* Michx)

Macromorphological description (November 1965)

- 0-0.5 cm L layer: Loose, horizontally piled, still resilient, brown leaves (sometimes curling up a little); presenting an undamaged aspect (round feeding-marks in parts due to the action of arboricolous fauna).
- 0.5-1.0 cm F₁ horizon: Grey, yellowish brown, more or less horizontally, densely piled, greatly weakened (fragile) leaf fragments. Covered

¹By "primary particles" are meant the organic particles in the excrements. The size of these primary particles is a measure of the fragmentation of the litter by the soil fauna. These primary particles may be clearly discernible pieces of tissue, containing cells, but also only pieces of cell membranes.

in places with blackish brown caked, fine faecal material. The horizontal position of the leaf fragments may be broken up in places, for instance by the activities of earth-worms and Tipulidae larvae, but also by thrushes looking for food.

- 1.0–3.0 cm F_2 horizon: A greyish brown horizon consisting (when moist) of loose, bumpy faecal material which has a certain cohesive quality on account of dense root growths (mineralization and good water-holding capacity; Fig.2). Only very few greatly weakened leaf fragments (3–5 mm) were found. The boundary with the F_1 horizon is fairly clearly marked.

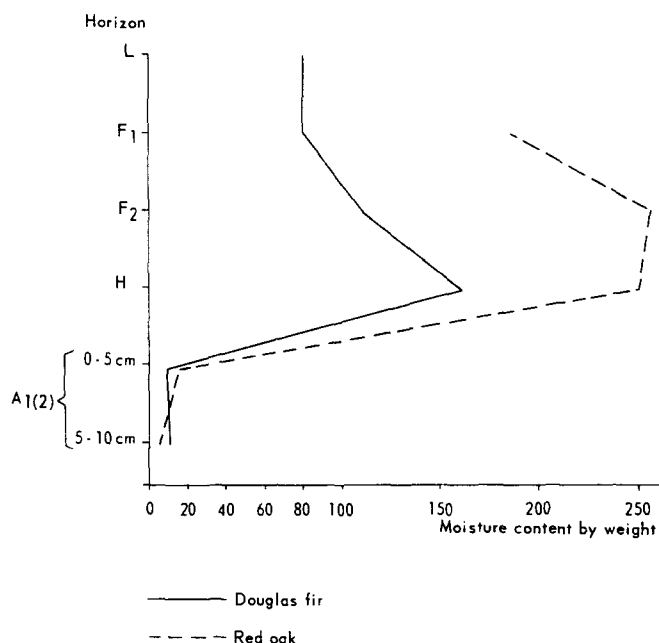


Fig.2. The soil moisture content by weight in the various horizons of the humus profile below Red oak and of the humus profile below Douglas fir. Both profiles are approximately at field capacity. It can be clearly seen that: (1) the faecal material retains the moisture better than the leaves and needles and; (2) in this respect differences exist between the excrements formed from Douglas fir litter on the one hand and from Red oak on the other.

- 3.0–6.0 cm H horizon: Dark brown to blackish brown horizon consisting entirely of loose faecal material which has a certain cohesive quality owing to dense root growths; leaf fragments are absent. Micromorphologically the horizon can be easily divided into an H_1 and an H_2 horizon; macromorphologically this is more difficult. The H_2 horizon is distinguished by the colour becoming increasingly black. Its underside forms a clearly defined boundary with the mineral profile.

6-15 cm A₁₍₂₎ horizon:¹ Humus having the consistency of small, black aggregates of from 100 to 500 μ , lying in between grains of sand with which there is no specific relation.

Genesis (Fig.3, 4)

L layer and formation of F₁ horizon

The L layer and the F₁ horizon act as protective layers (microclimate, breaking the force of the raindrops). Moreover, the leaves in the L layer cannot be directly devoured by the soil fauna. They must first undergo microbiological action and/or less tasty components have to be leached (Minderman, 1961; Van der Drift, 1965), as was shown in the case of Mycetophilidae larvae. These larvae quickly developed into adults on material from the F₁ horizon, but they refused material from the L layer and consequently died.

The microbiological action to which the leaves are subjected starts while the leaves are still on the trees; in the F₁ horizon this process has advanced so far that much of the mesophyll may have disappeared. But the epidermis and the ribs are then often still intact, one of the reasons being their high linked cellulose content, that is difficult to attack. Linked cellulose is highly resistant to microbiological action (Meyer, 1962; Babel, 1964). It is Meyer's belief that cellulose is linked with ligneous material. There are, in fact, indications that links do exist between lignin and carbohydrates (Richtzenhain, 1955).

The few excrements found in the F₁ horizon were from Diptera larvae; these excrements are, together with bacterial mucus, grains of pollen, algae, etc., devoured by coprophagous Enchytraeidae and Collembola (*Onychiurus quadriocellatus*). The coprophagous fauna further reduces the material and deposits its faeces (a mixture of dark-brown and much ink-black material) as pellets or shapeless masses in between leaf fragments, so that those fragments can adhere to one other. (Fig.4,e). Dark cakes of faecal material result from desiccation; accumulations along the ribs of the leaves may result from the action of rainwater.

It is noted, however that *Onychiurus quadriocellatus* also in only small quantities devours directly the leaves on the skeleton consumption (only a skeleton of leafribs, including the smallest ones, is left).

With the exception of epidermis and ribs, the leaf fragments in the F₁ horizon contain much material that is very susceptible to microbiological action and, as a result, the density and activity of the microflora in this horizon are generally greater than in all other horizons (Meyer, 1959). Among other things penetration of the leaves by moulds can be observed. Further, it was proved that the vitamin content is highest in those part of the humus profile in which the litter has only been little decomposed (Schmidt and Starkey, 1951).

¹Under the Netherlands soil classification system (De Bakker and Schelling, 1966) an A₁₍₂₎ horizon is an A₁ horizon in which, as a result of the onset of the podzolic process, typical features of an A₂ horizon are already present (see sections "Formation of A₁₍₂₎ horizon and origin of the humus aggregates" and "Formation of initial podzol-B horizon").

Formation of F_2 horizon

This environment is suitable for the smaller species of Diptera larvae owing to the densely packed layers of leaves in the transition from the F_1 - into the F_2 -horizon (Table I). As a result of the highly developed microbiological action the leaves have been greatly weakened and are, therefore, broken up into fragments. They have become suitable for consumption by "primary devourers"¹. That is why an intensive process of "Vermoderung" takes place on the underside of the F_1 horizon and within a distance of 1 cm the F_1 horizon merges into the F_2 horizon². The small Diptera larvae in particular are responsible for the process of Vermoderung, the bigger Tipulidae larvae being far less active in this way. *Oribatei* account for only little Vermoderung.

Of the small Diptera larvae, those of Mycetophilidae are active here in particular (Fig.5). The larvae, which grow fast, operate from a slimy funnel built by them. The funnel can be considered the larva's "home", which protects its tender skin against environmental damage and desiccation. Zachariae (1965) thinks that the funnels aid the larvae in their locomotion and other activities. They have, however, been observed to move with the greatest ease in all directions over a smooth surface. When they devour the leaves they leave "skeletons" of them or leave "holes" in them; at first, the ribs are not eaten, the midrib is not eaten at all. They also devour dead roots (though to a lesser extent) and mycelium (see also Kühnelt, 1961, p.275). The leaves are probably mainly fragmented into particles of approx. $80 \times 160 \mu$, a distinct tissue structure and cellulose often being left behind (Fig.7). So the larvae have to consume a lot of this material to obtain enough food to maintain their body growth. Retention values are not known, however. The material becomes stuck together with mucus in the intestinal tract and is deposited locally as globular excrements having a diameter of from 75 to 150μ . (Fig.6). The larvae are chiefly active on the underside of the F_1 horizon and hardly move about. As a result, excrements accumulate in the top of the F_2 horizon, where they fairly soon lose their individual shape owing to progressive microbiological action and percolating rain-water and turn into an easily malleable, smeary mass (Fig.4,a,f) These excrements are strongly attacked at various points in the profile by moulds, so that they disintegrate completely.

The bigger Tipulidae larvae also devour the leaves (eating holes into them) and produce round to spindle-shaped excrements of from $250 \times 350 \mu$ to $500 \times 600 \mu$.

The ovoid excrements of *Oribatei* ($50 \times 90 \mu$ – $120 \times 260 \mu$), found spread

¹In Kühnelt's classification according to feeding habits (1957), creatures living on dead vegetable material that has not been devoured before are called "primary devourers".

²Kubiena (1953, pp.46–50) understands by "Vermoderung" the break up of organic matter by the soil fauna, which as a rule does not incorporate the excrements in the mineral soil. The purely organic excrements consequently remain in the organic profile. If the excrements consist of a mixture of organic- and mineral particles these particles have been joined to each other only loosely. Contrasted with this is mull formation when, as a result of active biological homogenization, the excrements consist of a mixture of organic and mineral material and a mechanically inseparable complex between the humus substance and the clay substance has been formed.

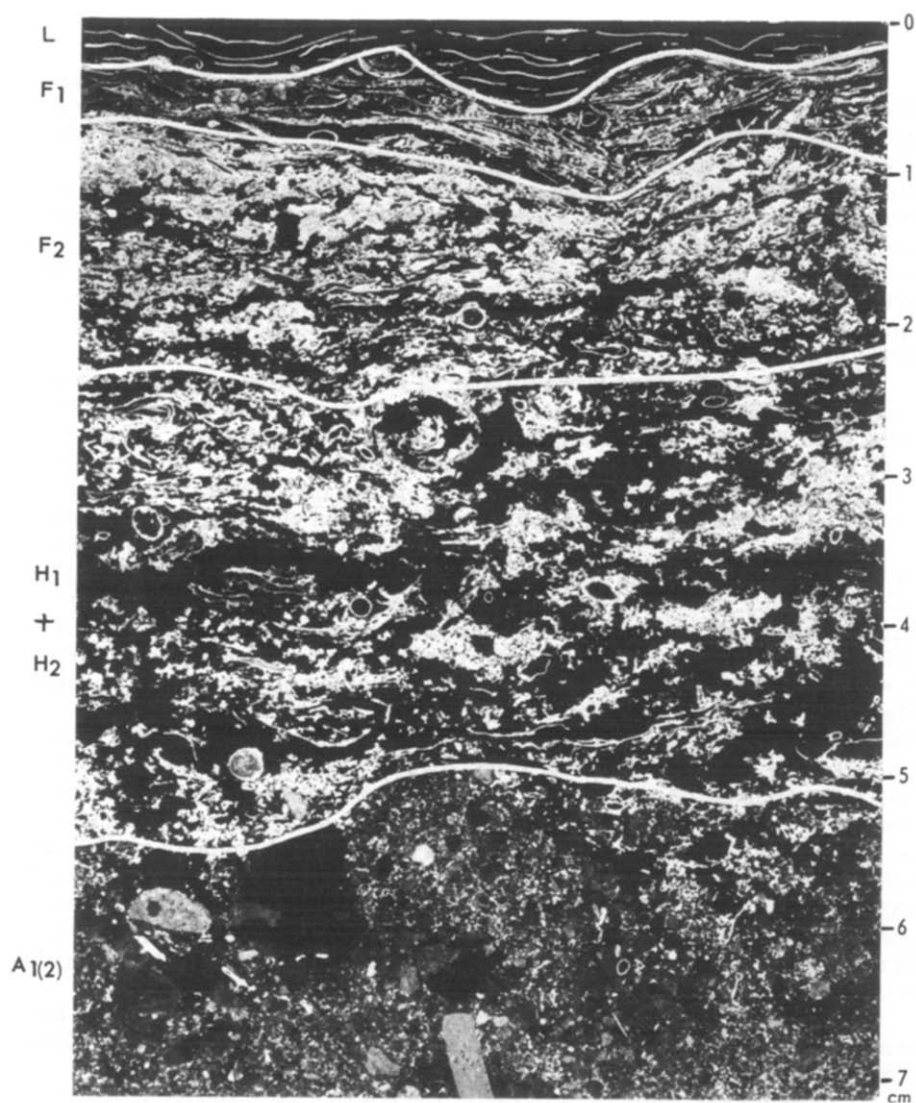


Fig.3. Photo of a mammoth-sized thin section of the humus profile below Red oak (2× natural size).



Fig.4. Micromorphological pattern of the moder humus profile below Red oak shown in Fig.3. The genesis of the profile is clearly seen in this figure. Excrements of: *a* = Mycetophilidae larvae; *b* = *Nothrus silvestris* ; *c* = *Nothrus silvestris* and *Rhysotritia minima* after exogenous and endogenous root glutting; *d* = *Dendrobaena rubida*; *e* = Enchytraeidae and *Onychiurus* 4-oc. Ageing excrements of: *f* = Mycetophilidae larvae; *g* = *Oribatei*; *h* = *Dendrobaena rubida*; *i* = faecal parts from the H-horizon illuviated into the A1(2)-horizon; *j* = root remnant (periderm) filled by fungi with black humin substances.

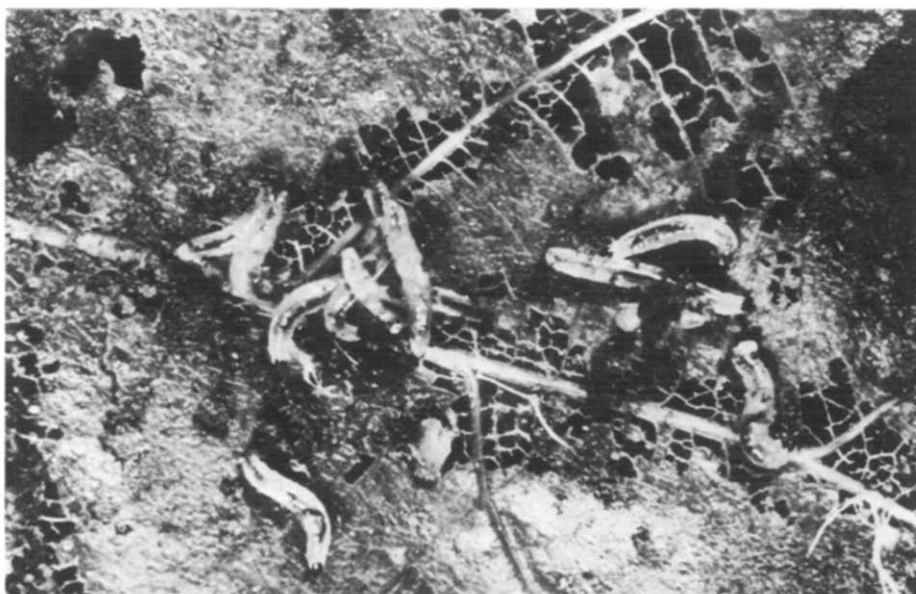


Fig.5. The microbiologically attacked leaves in the F_1 - and F_2 -horizon are devoured by Mycetophilidae larvae on the "skeleton"- and "hole" consumption pattern (2.9 $\times$ natural size).

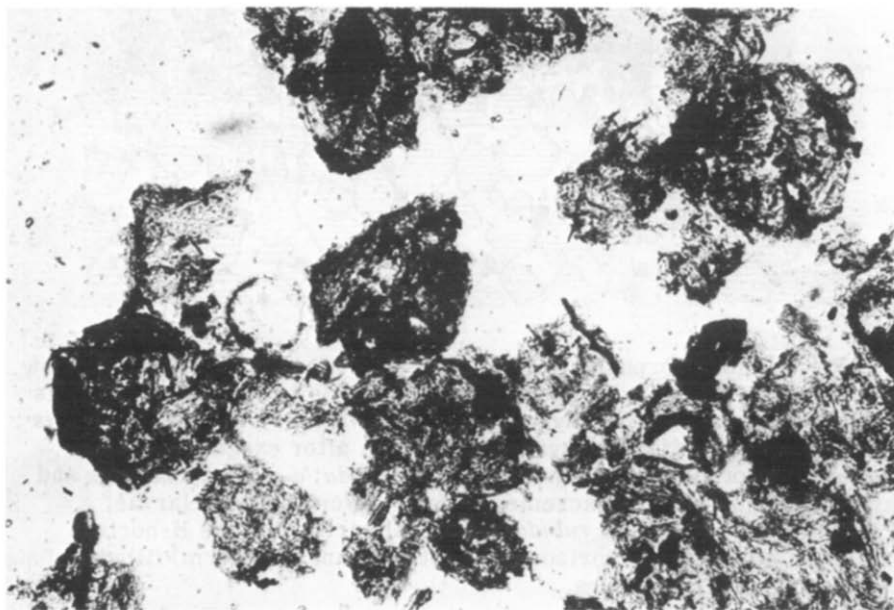


Fig.6. The larvae deposit their globular excrements where they eat which is difficult to see in the middle of Fig.5 (136.5 $\times$ natural size).

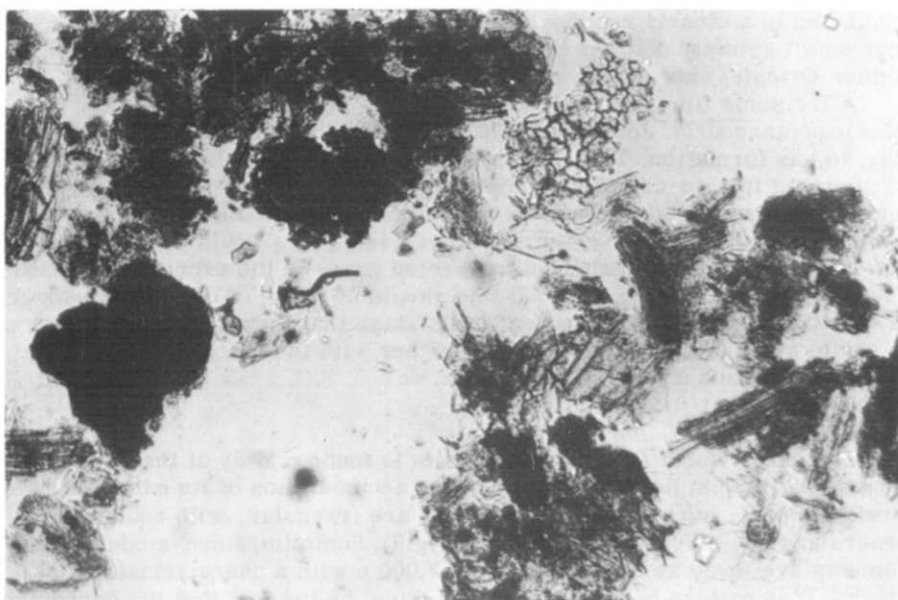


Fig.7. The globular excrements consist of bitten-off particles (primary particles) with a tissue structure which is still well defined. (152× natural size).

about, consisting of purely macrophytic material and of a mixture of macrophytic and microphytic material, are attributed to *Nothrus silvestris*, a "non-specialist" (Schuster, 1956 and our own culturing results). They devour the leaves on the skeleton consumption pattern or they devour almost the entire morphological underside and deposit their excrements where they are feeding or elsewhere (Fig.4,b).

Though *Nothrus silvestris* is a mobile Oribatid mite it is not impossible that part of the excrements in nidi may also be attributed to this Oribatid mite.

The size of the primary particles (averaging $12 \times 20 \mu$ and ranging from $< 4 \times 4 \mu$ to $100 \times 100 \mu$) consisting of remains of cell membranes, a few stomata, wood vessel fragments and fragments of mould hyphae, shows that intensive fragmentation has taken place.

The branches, roots and ribs mined into and filled with excrements of $30 \times 20 \mu$ consisting of pure, highly fragmented macrophytic material (remains of cell membranes and fragments of wood vessels) are attributed to the activities of the oribatid mite *Rhysotritia minima*, a devourer of macrophytic material par excellence (Schuster, 1956).

Oribatei excrements are exceptionally stable, as will also be seen in the section "Formation of F horizon" under Douglas fir; they can even pass intact through the intestinal tract of an earth-worm.

The breakdown process of *Oribatei* excrements is remarkable. They retain their original form for a considerable time and are affected by bacteria only gradually, which then may blacken them by forming black humic substances. Since they are highly resistant to action by moulds, they are

often found in a clearly recognizable form among faecal material from other small animals that has been affected by moulds. It is an open question whether *Oribatei* excrements contain persistent antibiotics.

After some time the *Oribatei* excrements fall to pieces (primary particles) spontaneously. Jongerius (1963) assumed that this is due, for one thing, to gas formation. This assumption is reasonable if the excrements are sheathed in a so-called peritrophic membrane. This is a semi-permeable membrane formed in the intestinal tract (pp.28). Supposing that this membrane is impermeable to oxygen and other gases, this would enable anaerobic bacteria from the intestinal tract to develop gases in the excrement, finally causing it to explode (Fig.4,g). All this should be seen, of course, in proper perspective. Generally it is not until this stage that they are consumed by the earth-worm *Dendrobaena rubida* together with the faecal masses of the Diptera larvae and a few leaf fragments.

Formation of H₁ horizon

The earth-worm *Dendrobaena rubida* is found mainly at the base of the F₂ horizon, for just below this there is an accumulation of its excrements (formation of H₁ horizon). Its excrements are irregular, with rounded corners and about $300 \times 300 \mu$ in size (Fig.8). Sometimes non-modelled excrements are found as large as $2,000 \times 2,000 \mu$ with a characteristic flow pattern. This pattern is formed, for one thing, by the fact that the excrement is passed by the worm in the form of a mass rich in water and containing

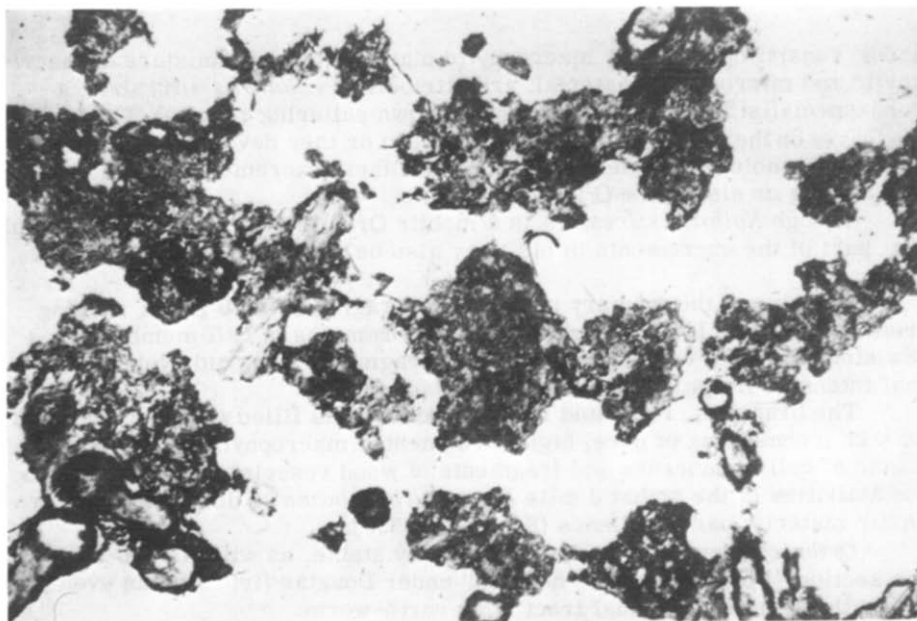


Fig.8. Excrements of the earth-worm *Dendrobaena rubida* in the H₁ horizon (35 $\times$ natural size).

consumed leaf fragments. The latter, though heavily eroded, have nevertheless retained much of their original form. The watery mass flows past the leaf fragments and so makes a certain pattern in them, which is finally fixed by desiccation (Fig.4,d).

The worm reduces the material to particles $< 15 \times 15 \mu$ and even $< 4 \times 4 \mu$, though whole *Oribatei* excrements and a few leaf fragments of more than 400μ may also be found in the excrements.

After a certain time the worms will again be able to consume their own faeces once the latter have been subjected to further microbiological action. It will be clear that the faeces grow increasingly richer in material that is not easily broken down (lignin, resins, waxes). Successive consumption will change the composition to a less degree. So the time span between two "consumptions" will increase. This explains why the H horizon consists of an accumulation of ever older earth-worm excrements and it is in this way that the series of faunistic processes are concluded.

Formation of H₂ horizon

At the base of the H horizon in the H₂ horizon it are only the moulds that continue the breakdown process, colour the material black and cause it to fall to pieces (Fig.4,d,h, 9).

From this section and the previous section it will be clear that we define an H₁ horizon as the result of accumulation of excrements by secondary devourers. An H₂ horizon is characterized by ageing (see corresponding sections on formation of H₂ horizon, and ageing under Douglas fir.



Fig.9. Ageing of excrements of the earth-worm *Dendrobaena rubida* in the H₂ horizon. As a result of severe fungal attack the excrements are broken up and turn black. The black coloration is associated with the formation of humic acids by fungi after autolysis (435 $\times$ natural size).

Oribatei are almost wholly responsible for the breakdown of roots in the entire H horizon, both by the mining of *Rhysotritia minima* and by exogenic devouring by *Nothrus silvestris* (and possibly also by *Rhysotritia minima*). In the roots these *Oribatei* do not have much competition from the rapidly developing and much more voracious Diptera larvae, which are seldom, found in the H horizon (Fig.4 c).

It is interesting to note that in some places roots (particularly smaller roots) are attacked by moulds, both in the F horizon and in the H horizon. The xylem shrivels up into a small core and finally vanishes completely. The periderm, however, remains intact and is filled up with dark humic substances formed by moulds. These substances (melanin?, Scheffer and Ulrich, 1960, p.173) are probably not formed until after autolysis. Finally, the moulds too, disappear, leaving a black tube. The production of humic substances can be so violent as to blacken even the surrounding faecal material (Fig.4,i).

Parts of larger roots and branches showing traces of cellulose (xylem) remain colourless. The contents of other cells, such as those of bark and the root centre, are coloured yellow or brown by the formation of humic substances (Kononova, 1961, pp.139-150; Babel, 1964). At this stage consumption by the soil fauna may take place. If it does not, the cells suffer from bacteriological action, as a result of which a number of them collapse. Others retain their form for a long time. It is only when they come into an "edge position" that they are transformed into an amorphous smooth mass.

If the larger root or branch is attacked by moulds, the effect of this may be so drastic that the root changes from macrophytic, as it were, into a microphytic texture in which the moulds are arranged in a pattern determined by the anatomic structure of the root, caused by the presence of pectin, cellulose, lignin, etc.

The organic profile described above may according to Kubiena (1953) be classified as "Feinmoder".

Formation of the A₁(2) horizon and origin of the humus aggregates

How do the humus aggregates get in among the sand grains? Although Vermoderung of the few roots in mineral soil does indeed take place, there is no mixing fauna. The aggregates are assumed to be very largely the result of illuviation from the organic profile lying on the mineral soil. It penetrates with the rain water that filters through (Jongnerius, 1957, 1961). However, this author had illuviation of excrements in mind, a view which can only receive partial support. For if we examine the aggregates of 100-500 μ , they are seen to be built up of aggregates of 20-30 μ , which in turn are composed of particles $< 12 \times 12 \mu$. According to Jongnerius, the aggregates of 20-30 μ are highly compacted excrements. The research showed, however, that the small *Oribatei* excrements are already relatively compact. The larger excrements, from other creatures, of say $500 \times 500 \mu$ would have to be very much compacted to attain such dimensions that transport would be possible. Moreover, the faecal masses are seen to break up in the H₂-horizon. It is, therefore, more likely that the primary particles or larger components (20-30 μ) of the excrements are illuviated in the mineral soil. Depending on the force of the water flow, the particles will be slowed down or halted at the spot where grains of sand touch each other. More particles will then arrive at this spot, whereby a larger aggregate will be formed if continuous humification occurs (Fig.4,i).

Formation of initial podzol-B horizon

At a depth of about 15 cm the aggregates turn yellow, break up and form a yellow "free grain, illuviation organan" of not more than 20 μ thickness round the sand grains and even "intertextic fabrics"¹. The cutan is built up of very small particles held together by a more or less amorphous material which originates from these particles. Deeper down in the profile the cutans disappear by mineralization. The entire decolorization process, formation and disappearance of the cutan takes place over a distance of about 4 cm in this soil. Jongerius (1961) came to the conclusion that the flow of illuviated particles is neutralized by breakdown (formation of yellow cutan) and even complete mineralization of the organic matter (disappearance of the cutan), which completes the breakdown process of the litter.

Iron very likely plays an important role in the formation and disappearance of the yellow cutan. There are indications that transport of small amounts of iron takes place up to a depth where coating occurs. So it is obvious that not all of the cutan disappears but in fact traces of the latter will remain. Accordingly, an initial podzol-B horizon is formed, so that the part between the initial B horizon and the H horizon may be referred to as A₁₍₂₎ horizon.

Arguments in favour of this theory are:

(1) The humus aggregates are very evenly distributed in the mineral profile (Jongerius, 1957).

Such an even distribution could not be caused purely by *Vermoderung* of local roots.

(2) If the primary particles in the H horizon are compared with the particles in the aggregates in the mineral soil, they are seen to be of the same size ($< 12 \times 12 \mu$).

If the particles in the mineral soil are extracted with the aid of 0.1N KOH, they are seen to possess a clearly vegetable tissue structure very similar to that of the primary particles in the H horizon. For the fulvic and humic acids formed on the surface of the particle can be dissolved in a weak alkaline solution, liberating the skeleton. The particles in the mineral soil are, thus, shown to be primary particles from the H horizon that have been further humified.

(3) How could a zone of yellow cutans be formed if no transport had taken place? If "*Vermoderung*" only occurs locally, the existence of this zone could not be explained.

(4) Wright and Foss (1968) proved experimentally that silt-sized (mineral) particles of from 2 to 50 μ easily moved through a sand column with leaching water.

¹In the morphological classification "free grain cutans" occur on the surfaces of grains, "intertextic fabrics" occur when skeleton grains are linked by intergranular braces (Brewer, 1964, pp.209, 170). On the basis of interpretation of the process of formation "illuviation cutans" are formed by movement of the cutanic material in solution or suspension and subsequent deposition (Brewer, 1964, p.224). Among the kinds of cutans distinguished into their material composition by Brewer (1964, pp.211-218) this author did not mention the kind of cutan described in our research. As it consists of organic material we propose to classify it as an "organan". There exist more kinds of organans.

DESCRIPTION AND GENESIS OF THE HUMUS PROFILE UNDER DOUGLAS FIR
(*Pseudotsuga menziesii* Mirb.)

Macromorphological description (November 1965) (Fig.10, 11)

- 0-2 cm L layer; Greyish yellow, clearly recognizable, loosely piled-up needles, most of which are still solid. They present a very 'worn' aspect. In some places the needles are covered with patches of blackish brown faecal material. Most of the needles are not fragmented. However, the base is often missing, having been lost when the needles fell from the trees, so that the reddish brown mesophyll is visible. This layer gradually goes over into the F₁ horizon.
- 2-3 cm F₁ horizon: This is packed tighter than the L layer, one of the reasons being that the majority of the needles have been fragmented (Table II). Many needles show a black line across: this is a weak spot where the needle is easily broken. A small quantity of faecal material is scattered among the needles as a dark-brown filling material; in consequence, the colour of this horizon is a mixture of greyish yellow and dark brown.
- 3-4.5 cm F₂ horizon: The large number of needle fragments are heavily masked by the dark-brown faecal masses, which give the horizon its colour. An in moist condition loose dark-brown horizon held together by roots.
- 4,5-6 cm H horizon: It still contains a few needle fragments and needles filled up with excrements among faecal masses. An in moist condition loose dark-brown horizon held together by fairly numerous roots. Sudden transition to the underlying mineral profile.
- 6-22 cm A₁₍₂₎ horizon: Humus in the form of black aggregates of 100-500 μ , which are hard when dry, loose between the sand grains. In the top 4 cm. mould threads may grow through the aggregates, hanging them up between the sand grains.

Genesis (Fig.10, 11)

L Layer

There are three possible reasons for the accumulation of needles in the L layer. Firstly, it may be explained by the fact that the needles cannot be easily attacked on account of their high C/N quotient.¹ Secondly, possibly by the presence of microbicides, which curb the activities of micro-organisms and soil fauna (Gisin, 1952; Winter and Willeke, 1952; Winter, 1955). Thirdly, owing to the loose formation of the stiff, rigid needles, the L layer will easily desiccate, so that the biological activity remains limited (Fig.10 and Table II). In this layer the tissue structure of many needles is still sound, with micro-

¹The needles have a C/N quotient of about 77. Compare the leaf of the red oak, which has a C/N quotient of about 53 (Kühnelt, 1961, p.258).

biological activity being indicated by the yellow-brownish cell contents or only the brown cell walls. Moulds are much less noticeable in this fir profile than in the profile under red oak. Brown mould hyphae penetrate the cell walls of a few needles only. The epidermis and the central vascular bundle are the least susceptible to attack. The epidermis and/or a transverse area in a few needles are blackened by an accumulation of humic acids resulting from microbiological activity. This area corresponds to the black line on the needles referred to earlier in the "Macromorphological description (November, 1965)" (Fig. 11f). The needles are so weakened at this spot that they easily break here (needle fragments in the F_1 horizon). In some needles the mesophyll has completely disappeared owing to microbiological activity. A number of needles in the L layer are thinly caked with black faecal matter from Enchytraeidae, which consume pollen grains, algae, micro-organisms, etc. adhering to the needles. A few traces of *Oribatei* excrements may also be found on them.

The activity of Tipulidae larvae, though small is striking. They bite off particles of the needles of between $85 \times 50 \mu$ and $170 \times 280 \mu$ and transform them in their intestinal tract into solid, round or spindle-shaped excrements of between $500 \times 500 \mu$ to $1,450 \times 870 \mu$, which they deposit all around. The primary particles still have a clear tissue pattern. Obviously, these creatures are not very particular about microbiological action previously undergone by the litter.

The fact that the excrements are scattered all around is proof of the mobility of these Tipulidae larvae. This and the larvae's size ensure that the needles in the L layer do not get too tightly packed. Another striking feature is the intactness of these excrements. They are remarkably stable and can easily be separated from the profile (Fig. 11,a).

Formation of F_1 horizon

The F_1 horizon largely consists of needle fragments that, their fragmentation apart, have not undergone much change, morphologically speaking with regard to the L layer. It would be wrong, however, to conclude from this that they have not changed much in their chemistry. Wittich (1939) has demonstrated that microbiological (i.e., chemical) attack is not always clearly demonstrated in morphological respect. Wittich stated that fir needles left on the surface did not show any anatomical changes after a period of 26 months, although 33.6% of the dry matter had already been lost.

The fragments are devoured to some extent by Mycetophilidae larvae and Phtiracaridae as well as by Tipulidae larvae.

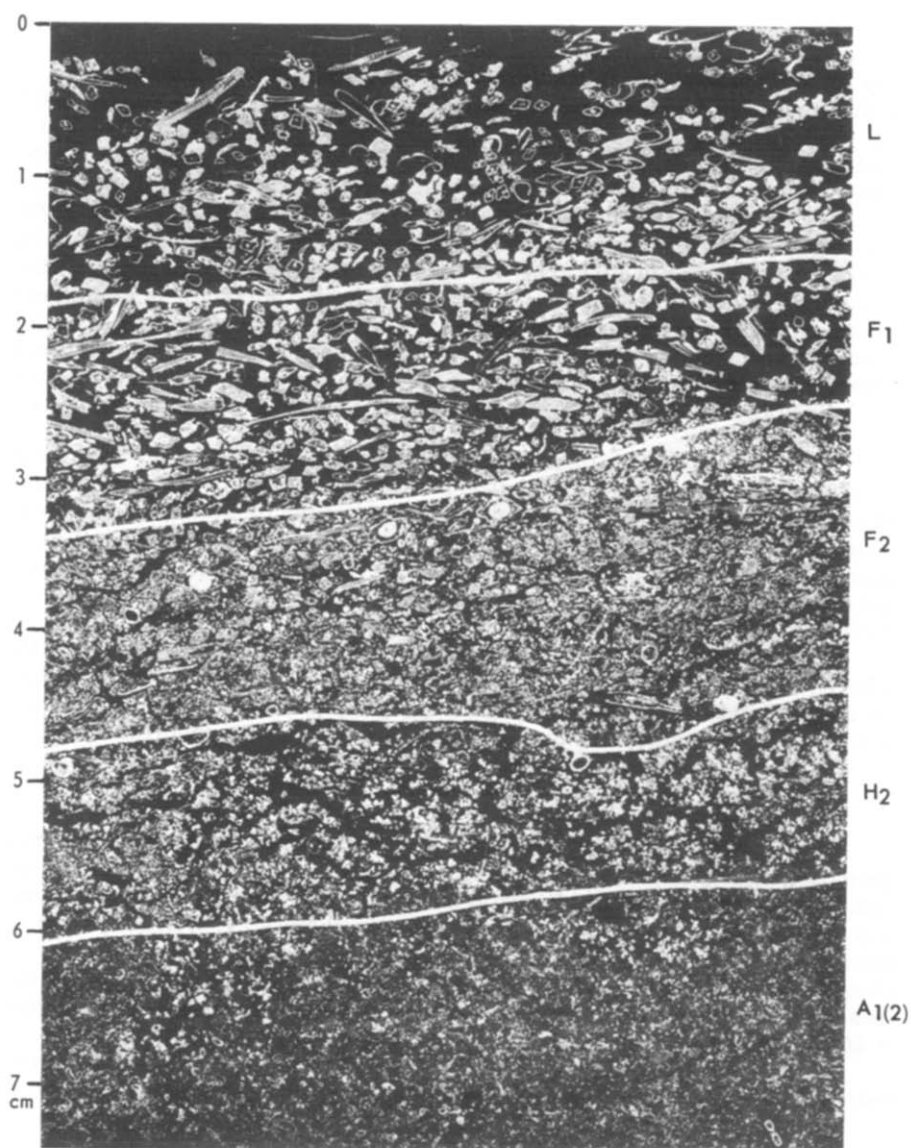
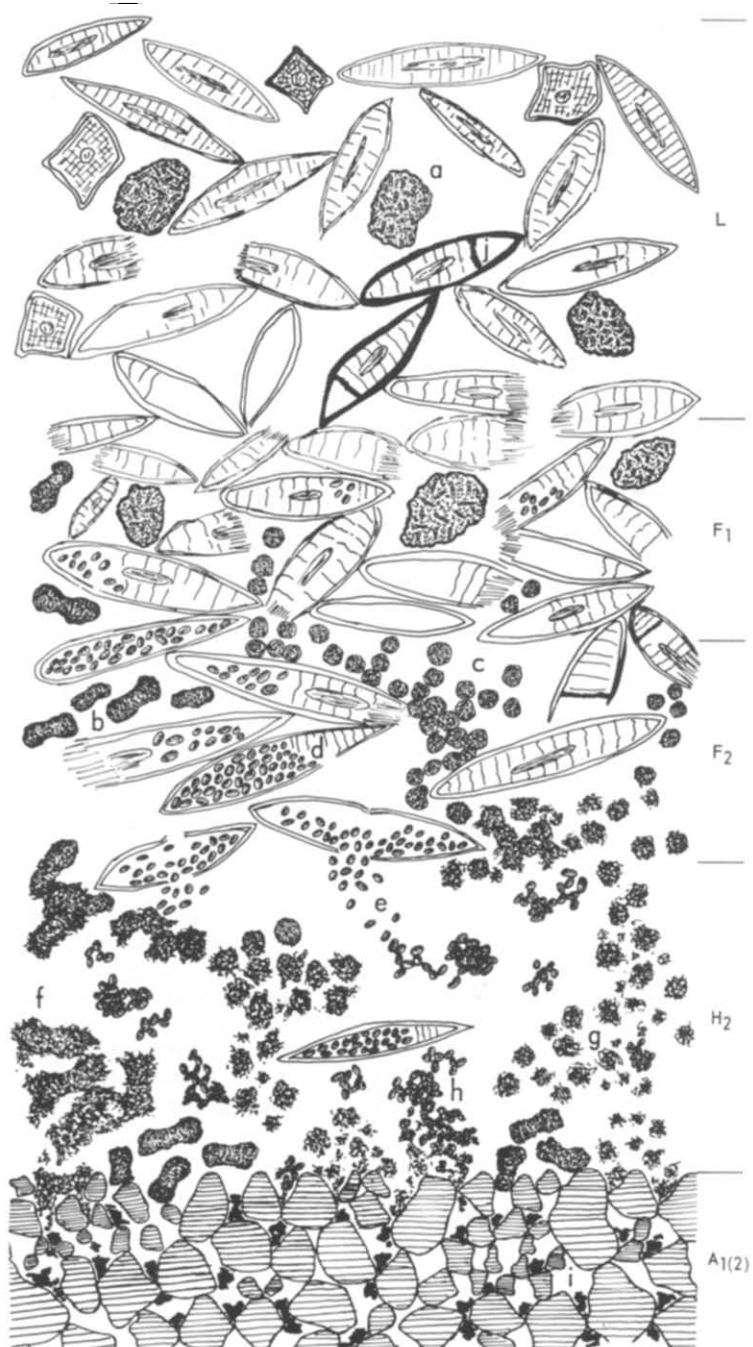


Fig.10. Photo of a mammoth-sized thin section of the humus profile below Douglas fir (2 $\times$ natural size). The fir needles have shrunk greatly owing to drying during preparation of the thin section.

Fig.11. Micromorphological pattern of the moder humus profile below Douglas fir shown in Fig.10. The genesis of the profile can be clearly seen in this figure. Excrements of: *a* = Tipulidae larvae; *b* = *Adela* larvae; *c* = Mycetophilidae larvae; *d* = needle mined by Phtiracaridae and filled with excrements; *e* = ageing of Phtiracaridae-excrements; outside the needles adhering of the excrements. Ageing excrements of: *f* = *Adela* larvae; *g* = Mycetophilidae larvae; *h* = Phtiracaridae; *i* = faecal parts from the H-horizon illuviated into the A(1)2-horizon; *j* = black humin substances in the needle.



Formation of F_2 horizon

However, Vermoderung only sets in properly, although less abruptly than in the profile under the red oak, at the transition to the F_2 horizon, where the quantity of material per unit of volume is high (Table II).

Mycetophilidae larvae and Phtiracaridae are particularly active there; the *Adela* larvae less so. Tipulidae larvae on the other hand, are possibly not active at all.

Phtiracaridae (*Steganacarus striculus*, *Rhysotritia duplicata*, *Rhysotritia minima*) consume macrophytic material. Moreover, they are the timber devourers among the *Oribatei* (Schuster, 1956). They mine into the fir needles and root and timber remains by eating a hole in this material which in size corresponds to the dimensions of their body and then consuming what they find inside. The space thus created is filled up with their characteristic, egg-shaped, solid excrements, varying widely in size from $12 \times 17 \mu$ to $200 \times 140 \mu$, depending on the species and stage of development of the individual mite. Since there is hardly any difference between the various excrements, it is difficult to say with certainty from which mites they originate. In cultures these mites in the adult, or almost adult, stage produced excrements of the sizes seen in Table III.

Abrupt changes in size of the excrements are often seen in a needle or root. This is no doubt due to the increase in size of the individual mite after it has cast its old skin (Zachariae, 1965). These excrements are particularly stable and retain their original character for a long time (Fig. 11d, 12, 13).

The humus-biological function of the Phtiracaridae consists mainly in a very thorough fragmentation of the litter mainly into particles of $< 12 \times 12 \mu$ ($\ll 4 \times 4-45 \times 28 \mu$). The material does not undergo much biochemical change during its passage through the intestinal tract (Schuster, 1956) as is also shown by the fact that the excrements have the same colour as the feeding substrate (Fig. 13). Accordingly, traces of cellulose and, according to Schuster, of lignin too, are still present.

The Mycetophilidae larvae consume the needles, as do the other larvae, by biting off small particles. They mine the needles in exceptional cases only, such as in the youth stage. The primary particles, which like these of Phtiracaridae have a resinous appearance, are mostly $< 12 \times 12 \mu$ (particles as large as 120μ are also found, however), have practically no tissue structure, are firmly pelletized in the intestinal tract and are finally expelled in the form of solid, characteristic, spherical excrements with a diameter of from 45 to 100μ , or cylindrical excrements of roughly $85 \times 170 \mu$. The larvae are rather sessile, staying at the transition of the F_1 to the F_2

TABLE III

Sizes of excrements produced by Phtiracaridae

Phtiracaridae	Size of excrements (μ)
<i>Steganacarus striculus</i>	between 57×34 and 100×75
<i>Rhysotritia duplicata</i>	200×140

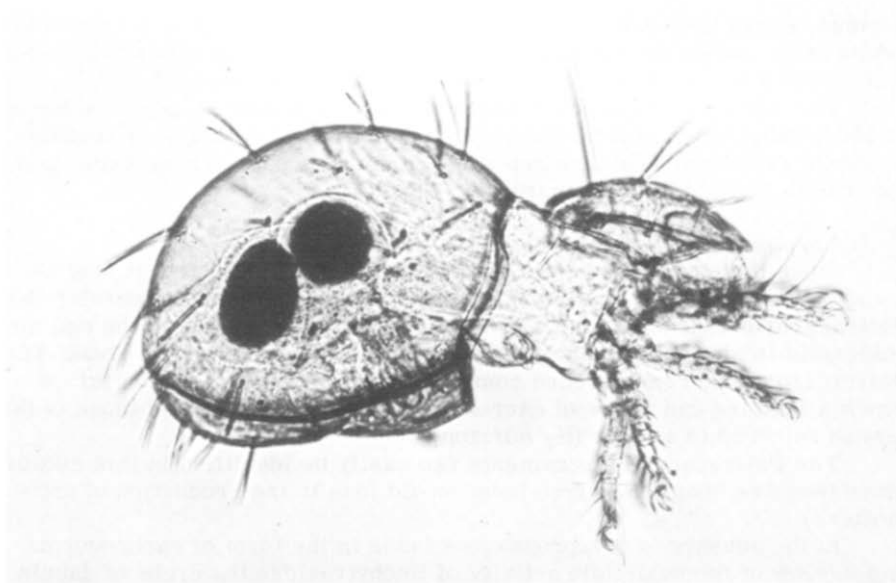


Fig.12. The Phtiracarid mite *Rhysotritia duplicata*. The characteristic ovoid excrements in the body (abdomen) can be clearly seen (102× natural size).

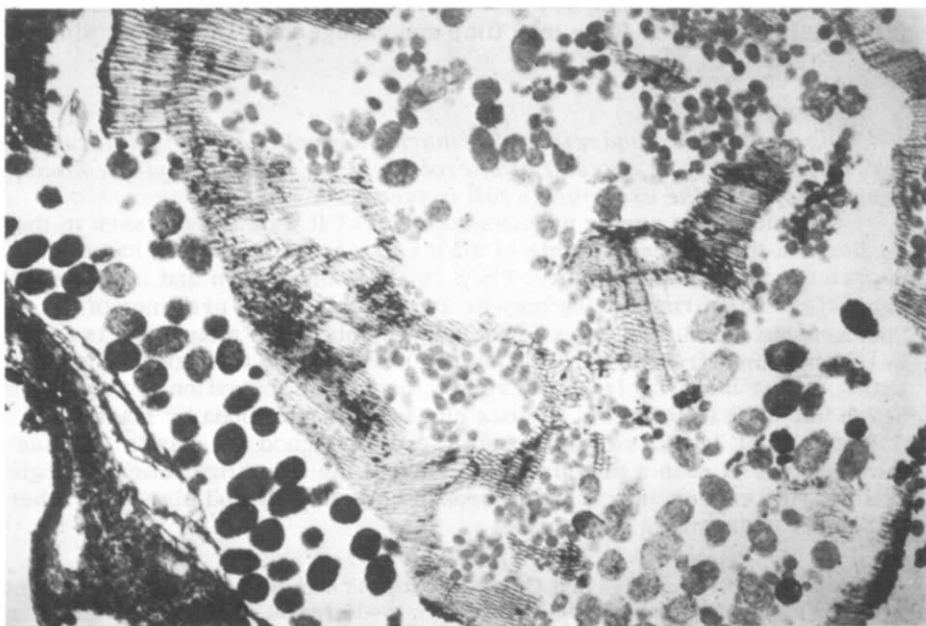


Fig.13. Dead root of branch in the F_2 horizon mined by Phtiracaridae and filled with their excrements. It can be clearly seen that the excrements are of the same colour as the substratum (35× natural size).

horizon, where they deposit their excrements (Fig.11). These excrements retain their individual character for a very long time and are not, therefore, transformed into a smeary mass, as is the case under the red oak.

The *Adela* larvae produce characteristic, cylindrical, solid excrements of $510 \times 260 \mu$, often contracted in the middle, in which there are clearly traces of cellulose. They are deposited in small groups. These excrements, too, retain their individual character (Fig.11,*b*).

Formation of H₂ horizon

Since the epidermis of the needles is not easily affected, it may be found deep down in the profile (H horizon). It then continues to envelop the Phtiracaridae excrements as a protecting mantle. However, in the end the epidermis is so weakened by microbiological action that it will break. The Phtiracaridae excrements then come out of the wrapping, as a result of which a mixture can occur of excrements of Phtiracaridae and those of the larvae referred to earlier (H₂ horizon).

The Phtiracaridae excrements can easily be identified in this mixture, since they are completely free from mould (due to the production of anti-biotics?).

In the absence of a coprophagous fauna in the form of earth-worms and in view of the negligible activity of Enchytraeidae the cycle of faunistic processes in the F₂ horizon has already been completed. Consequently, there is no H₁ horizon, and the F₂ horizon runs directly into an H₂ horizon (see section on formation of H₂ horizon under Red oak).

The litter in the H horizon is then further broken down by micro-organisms only, probably mainly by bacteria. Since fir material is not very susceptible to such action, the process is a slow one. The excrements therefore retain their form for a long time and change very little, they simply "age"¹.

Ageing

By "ageing" we understand the morphological changes that occur in the excrements solely as a result of microbiological, physical and chemical processes, until the excrements fall to pieces.

How does this ageing process take place? It was already seen in the F₂ horizon that the excrements of all the creatures mentioned had a high degree of stability and solidity. They retained their form and individual character. The firm packing may be attributable to the presence of a "peritrophic membrane" around the excrements. This membrane is formed in the intestinal tract to protect the latter from being damaged by consumed litter, for fir material is indeed rather tough. The formation of such a membrane has been observed in various classes of Arthropoda by Mason and Gilbert (1954). In this research, too, there were good reasons to surmise the presence of such a membrane. In view of the only slight microbiological activity, the excrements are only broken up gradually and slowly. In other words the excrements are durable.

¹Minderman (1961) reported that *Cephalcia alpina* excrements in larch woods in the province of Drenthe remained identifiable for 10-15 years. Although the "ageing" of excrements was also mentioned by Jongerius (1962), this author omitted to give an exact definition of this phenomenon.

As the attack by bacteria progresses, the excrement starts to soften internally, i.e., a phenomenon that could best be compared with the slow formation of a strongly viscous matter from a solid substance.

This "internal softening" is closely correlated to the development of bacteria colonies, breakdown products of the peritrophic membrane and formation of bacterial mucus and humic acids. To what extent the primary particles (e.g., resins) play a part in this remains a matter of conjecture. The primary particles become less easily identifiable in the excrements as a result of the above-described process. Finally, the excrements lose their form and individual character.

In the case of Arthropoda-larvae the excrements disintegrate more or less into semi-softened components.

In the case of Phtiracaridae excrements ageing is most characteristic. As long as the excrements are still in the needle, the morphological changes are only slight. After the "envelope" described earlier breaks or is broken and the excrements come free, the primary particles in it become less easy to see. After a time the excrements even acquire a smooth surface and look as if they were solid, in the meantime retaining their form and individual character. Next they start sticking together, thus forming larger aggregates. Finally, they flow together into a large, smooth, solid-looking mass. It will be clear that this agglomeration will change the distribution of the material, in such a way that more large cavities are formed in the H horizon (Fig.10). Fig.11, e, h, 14, 15, 16 clearly illustrate what happens.

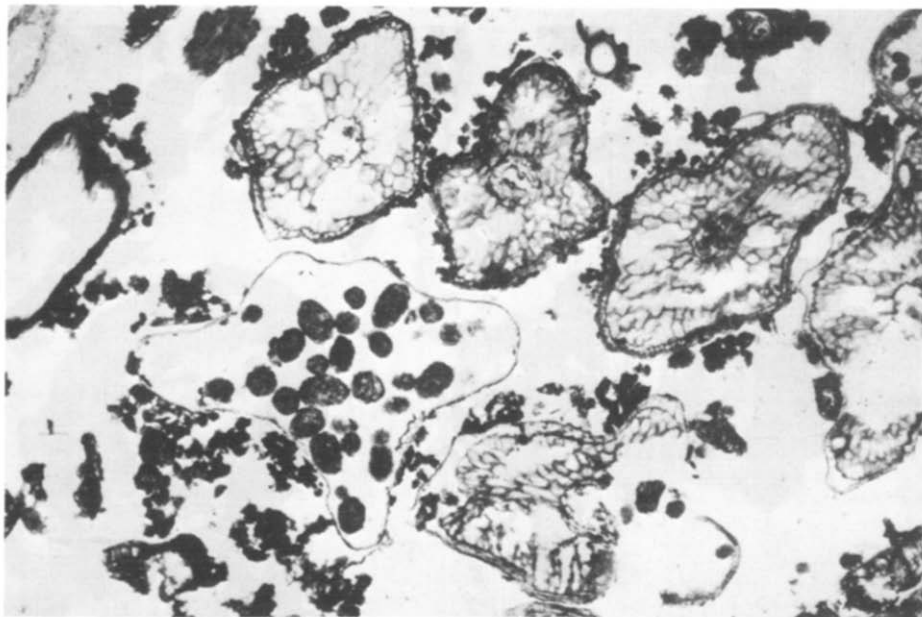


Fig.14. Stage one of ageing process of excrements of Phtiracaridae. A needle entirely mined and filled with excrements rests among micro-biologically attacked needles in the middle of the F₂ horizon. The epidermis which resists attack continues to form a protective mantle around the excrements (34.5× natural size).

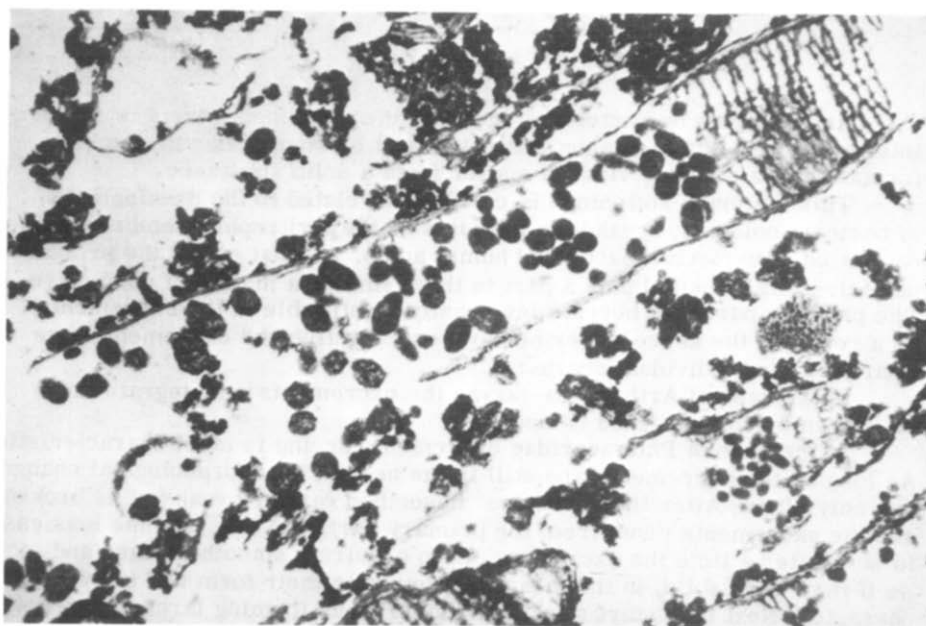


Fig.15. Stage two of ageing process of excrements of Phtiracaridae. At foot of the F_2 horizon the epidermis of the needles is so softened that it finally breaks and the excrements roll out. At this stage the latter still retain their individual character (34 $\times$ natural size).

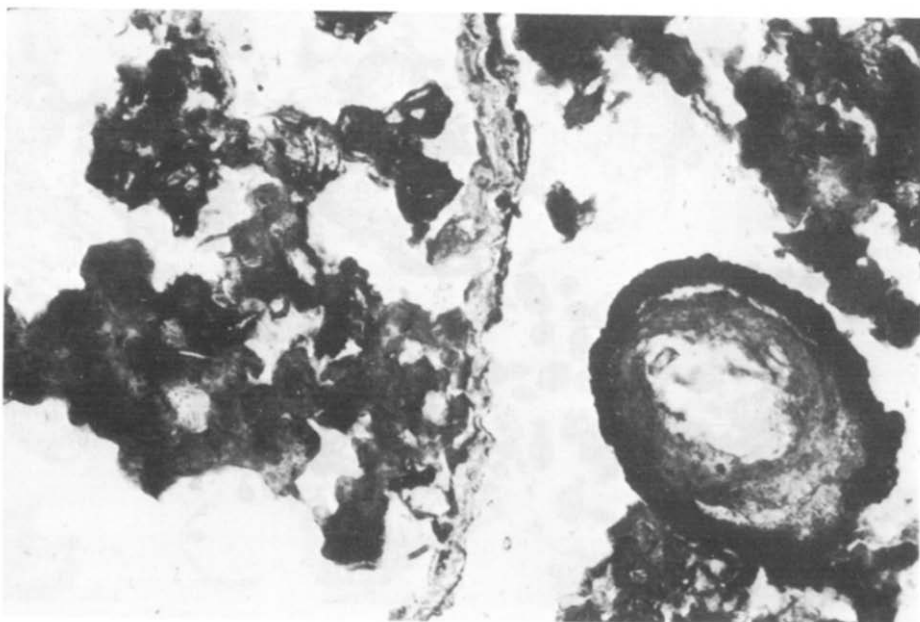


Fig.16. Stage three of ageing process of excrements of Phtiracaridae. Internal softening occurs in the H_2 horizon. The exposed excrements then adhere to each other to form larger aggregates and finally deliquesce to a single mass in which the outlines of the individuals can still be faintly distinguished (left on the photo). (140 $\times$ natural size).

Although not mentioned earlier, ageing also occurs in the profile under red oak, but in quite a different manner. There, *Oribatei* excrements break up spontaneously after some time, while moulds also play an important role in this profile, such as in the H₂ horizon (see under that heading).

A few needle fragments with tissue structure may still be found in the H₂ horizon. For this reason the organic profile described above can, according to Kubiena (1953), be classified as "Grobmoder".

Formation of A₁₍₂₎ horizon, origin of humus aggregates and formation of initial podzol-B horizon

For information about the origin of the humus aggregates in the mineral soil, reference should be made to what has been said earlier about this point in corresponding sections on Red oak. It should be noted, however, that the aggregates in the A₁₍₂₎ under Douglas fir are better formed, that they are hard when dry and that yellow cutans are not formed at a depth less than about 22 cm.

DISCUSSION

Effect of litter on the morphology of the humus profile

The difference in the extent to which litter of Douglas fir and that of Red oak are susceptible to attack has some interesting consequences for the morphology of the humus profile.

Differences in fauna

Vermoderung of the litter of red oak occurs mainly through *Diptera* larvae after which it is processed by earth-worms. Phtiracaridae devour mainly the more difficult parts such as larger roots, branches and leafribs.

Vermoderung of the Douglas fir litter, which is more difficult to break down, is largely done by Phtiracaridae, the creatures par excellence for feeding on material that is hard to consume. Since they live by mining, they are eminently suited to consume the interior of the needles in which at the same time they are better protected from desiccation. That seems the reason why *Steganacarus striculus* can subsist on fir needles, but not on oak leaves. *Diptera* larvae are much less at home among fir material and for earth-worms this fir litter is totally unsuitable, which explains their absence.

Differences in litter breakdown

Litter is devoured in different ways, even by the same species of creature.

Vermoderung of the litter of red oak is a relative rapid, while that of Douglas fir is a slow process. There is, in consequence, a difference in horizon thickness between the two profiles: the L layer under Douglas fir is relatively thick (2 cm), the H horizon, on the other hand, rather thin (1.5 cm). Under Red oak the L layer (0.5 cm) is relatively thin, the H horizon thick (3 cm) (see sections on macromorphological descriptions of humus profiles under Red oak and Douglas fir and Fig.3, 10). The general rule is that the more difficult the litter is to attack (whatever the cause may be), so the L layer is relatively thicker and the H horizon relatively thinner.

The fragmentation of fir needles by primary consumers, no matter

which they are, is stronger than that of oak leaves. Moreover, the structure of fir needles is at once entirely destroyed in primary consumption, except when they are consumed by large Tipulidae larvae, and the bitten-off particles often have a resinous appearance.

The bitten-off particles of oak leaves are larger and often retain a tissue pattern. This is possibly due to the fact that soft and easily transformable oak leaves are much easier to consume in large pieces than the stiff material of fir needles, which can only be consumed by systematic biting off.

Differences in excrements

It is particularly the stiff fir material that is firmly pressed into solid pellets of excrements in the intestinal tract of the creatures consuming it. As a result, and because of the fact that the material is not easily broken down, the excrements are durable, giving rise to a characteristic ageing process.

After consumption of oak leaf, well-formed excrements are indeed produced but they are not firm and lose their shape after a short time. Ageing under red oak is therefore less spectacular.

It is to be concluded from the sections on differences in fauna, litter breakdown and excrements, that although soil fauna plays an important role in the formation of the humus profile, it is the vegetation that ultimately determines the breakdown pattern. Vegetation determines by its characteristics what species of creatures can be present and in what manner the breakdown process will take place; in other words, the existing fauna is a function of the vegetation - *Steganacarus striculus* could not subsist on oak leaves, while *Nothrus silvestris* could not easily subsist on fir material. Earth-worms cannot subsist on Douglas fir material, they do subsist on oak material on poor sandy soil.

Effect of the fauna on the morphology of humus profiles

Soil-morphologically characteristic fauna

It was proved in the research that, although the environment of a profile is characterized by all its fauna only a few saprophagous members of that community are directly responsible for the morphology of the humus profile. It is, then, more efficient to characterize the humus profiles by the fauna directly responsible for them (characterization on a functional basis). In view of the determinative influence these creatures have on the morphology of the humus profile, they can be referred to as "soil-morphologically characteristic fauna". It should be noted that being soil-morphologically characteristic need not necessarily be correlated with the number of such creatures present. The deciding factor is that which they do in consequence of which the humus profile comes into being. Listing them in order of importance based on the quantities of devoured material (Tables I, II) in the profiles studied, we find the results as in Table IV.

TABLE IV

Soil - morphologically characteristic fauna listed in order of importance

Red oak	Douglas fir
Mycetophilidae larvae	Phthiracaridae:
<i>Dendrobaena rubida</i> (Savigny) 1826	<i>Steganacarus striculus</i> C.L. Koch, 1836
<i>Nothrus silvestris</i> Nicolet, 1855	<i>Rhysotritia duplicata</i> (Grandjean, 1953)
<i>Rhysotritia minima</i> (Berlese) 1904	<i>Rhysotritia minima</i> (Berlese) 1904
Tipulidae larvae	Mycetophilidae larvae
Enchytraeidae (mainly <i>Marionina clavata</i> Nielsen and Christensen, 1961)	<i>Adela</i> larvae
<i>Onychiurus quadriocellatus</i> Gisin, 1947	Tipulidae larvae
	Enchytraeidae (mainly <i>Cognettia sphagnetorum</i> (Vejdovsky) 1877)

The soil fauna as a soil forming factor

In this publication we suppose it is allowed to designate horizons in the humus profile. However, we should like to point out the fact that in literature is spoken of layers as well as of horizons. In pedology by horizon is meant the more or less, parallel to the earth-surface, like a layer-looking resultant of the soil forming processes (pedogenesis). A layer (stratification) on the other hand is the resultant of geological processes.

Zachariae (1965) states the grounds for designating layers and avoids purposeful the designation horizon as this latter one has been allied too closely to the genesis of the (mineral) soil profile. As Zachariae in studying the humus profile stresses the soil fauna and to the latter the building up of the humus profile is a datum, which will not change during the short life of the creature, this author prefers to speak of layers (only meant as a grouping of the space to live in).

However, there exists a strong resemblance between the pure pedogenetic processes and the processes which create horizons in the humus profile. For a soil-forming process is a process which occurs to the soil components caused by interaction between the soil-forming factors (parent material, climate, topography, biosphere, man, time) by which a horizon comes into existence (Jenny, 1941, pp.15, 203).

The investigation proved that within the humus profile, there occurs something like that, in which horizon-forming processes are, e.g.: the transformation of leaves into excrements, ageing, eluviation and illuviation of organic particles. The soil-forming factors do cause these processes as much as they cause the well-known pedogenetic processes in the mineral soil.

Although seen from the soil zoological point of view it is clear that one considers the space of living the motive of Zachariae that the creatures lifetime is too short is not sound when it is seen from the pedological point of view. For the horizon-forming process concerns generations of creatures. Moreover this author is not quite logical as he pays homage to the (laudable) principle the building up of the humus profile not only to base on a

fauna analysis, but also in studying the building up of the humus profile starting from the tracks of the fauna in the profile (and just that is the genesis).

Based on the above one may fix that the humus profile has been built up of horizons, except the L-layer.

Spatial building up of moder humus profiles

The Tables I and II suggest there is in the organic profile a rule in the distribution of the organic material to depth. It is striking that the quantity of material per unit of volume is relatively low in the L-layer and highest in the uppermost part of the F_2 horizon to decrease again in the F_2 - and H-horizon.

It is obvious that this way of distribution correlates with the processes characteristic for moder humus profiles. In the L-layer the litter is piled up loosely. By settlement, non-zoogenic fragmentation and especially the intensive fragmentation and transformation of litter into excrements by a rather immobile fauna in the transition from the F_1 -into the F_2 -horizon the density increases. The decreasing density deeper in the F_2 - and H-horizon can be explained by mineralization and eluviation.

ACKNOWLEDGEMENTS

I should like to thank Dr. A. Jongerius (Head of the Department for Micropedology of the Netherlands Soil Survey Institute at Wageningen) and Dr. J. van der Drift (Head of the Department for Soil Biology of the Institute for Biological Field Research at Arnhem) for their co-operation and hospitality, without which this research could not have been made.

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